ESTIMATES OF POPULATION DENSITY AND DISPERSAL IN THE NATICID GASTROPOD, POLINICES DUPLICATUS, WITH A DISCUSSION OF COMPUTATIONAL METHODS[1]

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This paper reports an attempt to use marking of individual snails and capture-recapture methods to assess population density and rates of dispersal in a littoral population of *Polinices duplicatus* at Barnstable Harbor, Cape Cod, Massachusetts. Earlier work by the present authors on the ecology of the infauna of the sand-flats in the Barnstable area (D. C. G.), and on the general biology of *Polinices* spp. (W. R. H.), had indicated both the importance and the difficulties of density estimates in populations of *P. duplicatus*.

Standard methods such as direct counting of quadrats are completely unsuitable, as preliminary surveys for the present work showed. Some of the difficulties are those which would arise with any moderately large-sized, and relatively widely dispersed animal capable of burrowing—others are peculiar to *Polinices,* and result from aspects of the behavior of "moon-snails." For example, they can burrow deep into the substratum, can remain immobile for considerable periods, and may show marked tidal periodicity. Thus the present study showed that the number of animals visible at or near the surface of the sand at any one time is but a fraction of the total inhabiting the area.

However, it is important to attempt an accurate assessment of the population density in *Polinices*—and in other "ecologically difficult" species such as the horse-shoe crab, *Limulus.* In many areas of tidal flats around Cape Cod and elsewhere, such animals are among the important "terminal consumers" in the majority of infaunal associations of invertebrates. Further, the commercial importance of naticid species as pests of shell-fisheries has long been recognized.

Techniques of capture, marking, release and recapture have been used extensively in studies of birds and small mammals, and of insects such as Lepidoptera and tsetse-flies. Such methods were developed independently by Jackson (1933, 1937, 1939, 1948) working on tsetse-flies, and by Lincoln (1930) working on ducks. The former author, in association with R. A. Fisher, evolved a more sophisticated arithmetical treatment which allowed estimates to be made on populations of changing density. Subsequent work on Lepidoptera (Fisher and Ford, 1947; Dowdeswell, Fisher and Ford, 1940, 1949) utilized "trellis" arrays and allowed estimates of death-rates and emergence-rates. Some of the complications

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arising from differential behavior within the populations studied have been discussed by workers on small mammals (for example, Evans, 1949, on house mice) and on insects (for example, Ayre, 1962, on ant colonies). The significance of the different methods of analysis used on capture-recapture data has been considered by Schumacher and Eschmeyer (1943), Leslie (1952; see also Leslie and Chitty, 1951; Leslie, Chitty and Chitty, 1953), DeLury (1958), Turner (1960) and Andrewartha (1961). Treatments which can be used to estimate the bias and precision of the results obtained have also been developed (Bailey, 1951, 1952), and the methods applied to a variety of terrestrial vertebrates and insects. However, capture-recapture methods have not previously been applied to any extent in studies of marine benthic animals.

Methods

Use of capture-recapture methods to assess population density is based on a number of assumptions, and this population density experiment on *Polinices duplicatus* was designed to satisfy as many of these as possible. Preliminary surveys and assessments of population density and dispersal by other methods made this feasible. The most important condition is that the marked animals after their release become homogeneously dispersed through the unmarked population before resampling. On the other hand, the simplest methods of calculation involve the assumption that resampling takes place immediately after release of marked animals (thus before the population is altered by births, deaths, immigration or emigration). Sampling only adult snails and using a time interval of 24 hours removes the complications due to births or deaths in a long-lived (4–7 years, Hunter, unpublished) animal like *Polinices*. The accuracy of population estimates is most greatly increased by having second and third recaptures at exactly equal intervals of time, and further increases in accuracy can be effected with further recaptures. However, the increased accuracy of ten recaptures over nine is not great, and considerations of effort to be expended made a six-day capture-recapture series optimal for the present work. A final assumption in this work is that marked individuals are identical in terms of life expectancy and behavior with unmarked individuals, and that the actual marks are permanent. The conditions of survival of individual snails and of marks are certainly satisfied for the six-day period, but a temporary disturbance of behavior resulting from the handling involved in marking was detected. This is discussed more fully below, and arithmetical procedures which circumvent the effects of this behavioral change on population assessments are set out.

The populations of *Polinices duplicatus* in Barnstable Harbor are of enormous extent, and a limited area for the capture-recapture experiment had to be set out. Its size had to be practical for collection of all snails sighted, that is of all the proportion of the population visible at or near the surface. On the other hand it had to support a sufficient number of snails both to avoid the complications of "patchy" distribution and to give the increased accuracy resulting from samples of 100 or more. Lastly, if the rate of capture, and the total area collected, could be adjusted so that the recaptured (marked) snails numbered between 5% and 25% of each sample subsequently captured, the accuracy of the population assessment would be relatively high.

In the early summer of 1962, direct counting of quadrats was carried out in several parts of Barnstable Harbor, and the numbers of *Polinices* were counted along tidal contours to find an area of relatively uniform density. The locality chosen was on the southern shore of Barnstable Harbor, about 400 meters east of the dredged channel into Maraspin Creek, on a relatively uniform substrate of muddy sand, at latitude 41°42.6′N, and longitude 70°17.9′ W. The size of the area chosen to fit the conditions described above (*i.e.*, with sufficient population numbers, but small enough to make recapture practical) was 1600 square meters, being a square 40 m. by 40 m. The tidal range at this locality is 6.8 feet at neaps and 13.1 feet at springs. The experimental area, laid out normal to the littoral contours, was just covered at low water of neaps, and was totally exposed only during spring tides. The area was actually marked out as a central 20-m. square (400 sq. m.) within the main 40-m. square (1600 sq. m.) by eight permanent steel pegs. During each days' work a six-foot wooden stake was placed at each peg. The dispersal experiment discussed later was carried out around a single peg which was placed about 250 m. west of the main experimental area.

Since the whole process of capture, marking and redispersal took about four hours, and since it was planned to sample at every second low tide for six days (to maintain a constant interval of 24.8 hours between samples), the choice of dates was limited. The main series was run on August 8 through 13, 1962 (hereafter referred to as days I through VI), actual times of predicted low water ranging from 1215 to 1640 hours D.S.T. The tidal cycle in Barnstable Harbor is slightly modified from a single semi-diurnal pattern, and the afternoon range is less than the overnight.

On each day the eight stakes were placed about two hours before low water, and collecting of the sample of *Polinices duplicatus* was begun immediately. All collecting was done by the authors alone, in less than two feet of water and during the ebbing tide. The area of the main (larger) square was repeatedly traversed in a series of strips (about 1.6 m. wide), with a regular alternation of starting point between the two collectors. In fact, no bias occurred between them with regard to total numbers of animals, size of animals, or number of marks recaptured. Every snail sighted in the area was collected, until no sightings occurred over a 10–15-minute interval. and this always resulted in a sample of over 150 snails. The time taken for this collection varied somewhat with visibility (*i.e.*, weather and extent of wave action) and, under better conditions, occupied about 90 minutes. On one occasion (day IV, see below) conditions were so bad that collecting had to continue for about three hours (*i.e.*, including a period of the rising tide). The snails collected were stored in buckets of frequently changed shallow water. Sorting and marking were carried out on a small table set up in the water near the sample area. Sorting consisted of removal of undersized (< 2 cm.) specimens of *P. duplicatus* and all specimens of the closely related *Lunatia heros* which had been picked up accidentally. These "rejected" snails were dispersed some distance away. At this stage on days II through VI, all marks recaptured were counted, and the snails then given the appropriate mark for that day. The actual numbers at this stage were: I—142, II—132, III—145, IV—157, V—161, VI—136. Preliminary marking experiments had been carried out earlier in the summer on over 100 snails. Test marks on all parts of the shell of about 15 model dopes, nail polishes and marking pens showed that seven types would survive for over three weeks even on the apex of the snail. To avoid any differential predation of marked snails, the mark in the density experiment was placed in the umbilicus of the shell which is not normally exposed in life, either to predators or to abrasion in the sand. In fact, of the specimens marked during the main series, at least three had clearly distinguishable marks when recovered eleven months later, and one after three years. More confidently than is usual in such experiments, it can be assumed that no

TABLE I

Data from density square

Day		I	II	III	IV	V	VI	VIF
Number captured		(174) 142	(141) 132	(164) 145	(177) 157	(185) 161	(183) 136	(420+x) 420
Unmarked		142	129	122	99	94	89	147
Single Marks	I (Pink)		3	19	15	21	8	36
	II (Red)			3	19	14	11	48
	III (Black)				22	24	10	45
	IV (Green)					3	9	46
	V (Orange)						1	35
Double Marks	I + II			1	1			0
	I + III					3	3	11
	II + III				1		1	2
	I + IV					1		5
	II + IV						1	10
	III + IV						2	15
	I + V							6
	II + V							3
	III + V						1	7
	IV + V							1
Triples						1[A]		3[B]
Number marked		142 Pink	132 Red	145 Black	157 Green	161 Orange		

Notes: Numbers in brackets above second row are actual captures including *L. heros* and undersized specimens of *P. duplicatus*.

[A] One triple: I, II and III.

[B] Two triples: I, III and V; One triple: II, III and IV.

marks were abraded or otherwise lost during the six days of the principal observations.

The marking was always carried out in the same way. Lots of 10 snails each were removed from water in the storage buckets and caused to withdraw totally. Their shells were then dried with paper towels and the umbilical area cleaned with a little alcohol, care being taken to avoid the aperture and operculum of the shell. The alcohol-cleaned spot then received the day's mark, and was allowed to dry for a maximum of four minutes before the snails were returned to the storage buckets. Periodically, batches of 30–40 marked snails were randomly distributed through the dispersal area (*i.e.,* the inner 20-m. square). The rationale for this dispersal will be discussed below. Thus, the snails were out of their habitat for 1.5–2 hours, but out of water only during the actual marking, for a maximum of eight minutes. The arithmetic procedures employed in assessing population density from the data thus collected will be discussed in the section on analysis and interpretation.

An experiment on rates of dispersal in *P. duplicatus* was carried out in an adjacent area during the last three days of the main capture-recapture series. A total of 393 marked snails was released around a single fixed point and their dispersal followed visually for 30 minutes. On two subsequent days concentric circles were staked out at 1, 2, 3, 4, 5, 7, and 10 meters from the fixed point, and the numbers of marked and unmarked specimens of *Polinices* within each annulus recorded. Two types of marks were used. Of the 393 marked snails, 105 were freshly marked in the field with a single black line on the apex, while the remaining 288 had been captured on the previous day, taken to the laboratory, marked with a black cross and released after 24 hours.

In all, 1237 snails were marked in these series of experiments. On the last day, after the regular sampling, as many snails as possible were captured over a period of hours in both the "density square" and the "dispersal circle." Of 737 snails marked and released in the density experiment, 273 snails bearing 339 marks were recaptured and taken to the laboratory where maximum shell diameter was measured. Of the 393 snails marked and released in the dispersal experiment, 156 were finally captured and measured. Almost a year later, three collections totalling 402 snails were made in the density area and two marked snails were collected. At the same time, but independently by Dr. Ralph I. Smith, a further marked snail was found about 400 m. away. Three years later, a total of 183 snails collected in the general area included one marked snail (from the main density experiment), which was found about 300 m. from the density square.

Results

The capture-recapture data from the density experiment are set out in Table I above. The numbers in brackets in the column of total captures represent the actual numbers collected including undersized specimens of *Polinices duplicatus,* and specimens of the closely-related *Lunatia heros* (see Methods above). As can be seen, the experiment was relatively successful in terms of satisfying the several conditions for greater accuracy outlined above. For example, the average number captured and marked in the regular samples was 147 and, with certain exceptions, the numbers of each mark recaptured made up 7.7% to 19.3% of the samples. As noted above, there was no detectable bias between the two collectors in any respect. From the data, there is no indication that any individual animal exhibits an increased or decreased likelihood of capture. Certain data in Table I are significant in this respect. An excess of double marks in any group captured would indicate that there were individual snails more prone to capture. This can be tested in several ways. For example, if we consider the column for the regular captures of day VI, total captured snails were 136, of which 39 bore a single mark and 8 double marks. On that day the cumulative total of marked individuals at risk was 586 (by addition of the appropriate values for unmarked snails newly marked each day) and the corresponding number for double (and triple) marks at risk was 143. Thus the capture-ratio for all marks was 47/586 or 0.080 and for double marks 8/143 or 0.056. Applied at several levels, these sorts of ratios do not indicate any group of snails more prone to capture. On the other hand, estimates could be also biased by some individuals being *less* readily captured. A crude test of this, although it involves a nearly circular argument, can be justified by the fact that *all* individuals captured on days I through V were marked. Using the line for the total captures of day VI (that is, VIF), the unmarked captured number 147, and several of the different estimates calculated below (and based on the entire day's collection) place the total snail population in the square at about 990 individuals. Assuming this to be correct, there would be 404 unmarked individuals at risk on day VI; thus the estimated capture-ratio for unmarked individuals was 147/404 or 0.36, while the ratio for all marked individuals was 273/586 or 0.47. This could demonstrate the absence of excessive bias resulting from individuals being less readily captured, *except for* the hypothetical extreme case where a significant proportion of the population remained undetected for more than six days. On the basis of observed behavior, this extreme hypothesis is unlikely. It is worth emphasizing again that it was totally impossible for the marks in the umbilicus to influence the collectors during the capture of expanded snails.

One source of bias was detected subjectively during the sampling, and is revealed in the data of Table I. The normal behavior of moon-snails is temporarily disturbed by the handling involved in capture and marking. After release in the inner dispersal square, such snails usually re-expand within eight minutes (all do within twenty minutes), and soon burrow deep into the substratum where they remain expanded but immobile for some time. Of course, in this expanded but buried state they are not liable to detection and capture. At first, it was known only that this period of immobility extended for more than 24 hours but less than 49.6 hours (or four tidal cycles). Then it was observed that, although snails marked on the previous day were not present in any numbers during the regular sampling, that is, during a 90-minute period *before* the time of low water), they became obvious among the many active snails on the surface during the two hours *after* the tide had begun to rise. In other words, recovery from marking trauma is complete in just over two tidal cycles, or about 25.5 hours. There is other evidence that a proportion of the population will always become more active immediately after inundation by a rising tide, and that this can involve a condition of temporary hyperthermia (Hunter and Apley, 1965). The effect of trauma is reflected in the number of marks recaptured after only one day (Table I). For example, the number of mark I captured on day II is relatively low. (For convenience, we can refer to R_{xy}, being the number of recaptures on day y, bearing a mark from day x.) Thus R_{12}, R_{23}, R_{45} and the regular R_{56} are all relatively low. On the other hand two collections do not show this effect: day IV and the final collection of day VI (VIF). Collecting on both these occasions extended into the first hours of the rising tide: on day IV because of bad weather conditions slowing the collecting rate, and later on day VI as a result of the deliberate collection of the large final sample over a period of hours. In several of the calculations below, the data of R_{12}, R_{23}, R_{45} and the regular R_{56} are rejected as biased, while R_{34} and the final R_{56} can be utilized, along with the other data where more than one day has elapsed between marking and recapture, such as R_{15}, R_{25}, R_{35} etc. Finally, the marks borne by the four snails recaptured with triple marks are detailed below

Table I, and have to be incorporated into the number of single and double marks recaptured in certain of the calculations below.

The data from the dispersal experiment are summarized in Table II. Although less successful than the density experiment, and hardly a complete measure of the possible rates of dispersal, a few significant facts emerge. In the first 30 minutes, 376 of the 393 individuals had expanded and righted, and > 200 were out of sight, having burrowed into the sand. The three specimens in the 2.0–4.0-m. annuli were known to have expanded and "sailed" with the longshore tidal current, but several had crawled > 1 m. and at least two had covered 1.75 m. Comparison of the sighting records (after two tides) and the final collections (after four) shows that line-marked specimens recovered more rapidly than the X-marked ones did from their

Table II

Data from dispersal experiment

Annuli in meters		0.–0.5	0.5–1.0	1.0–2.0	2.0–3.0	3.0–4.0	4.0–5.0	5.0–7.0	7.0–10.0	Totals
At release	Cross	288	0	0	0	0	0	0	0	288
	Line	105	0	0	0	0	0	0	0	105
	Unmarked	?	?	?	?	?	?	?	?	?
After 30 min. Sight records	Cross, Line	(16*)approx. 100–150†		18†	2†	1†	n.d.	n.d.	n.d.	137–187†
	Unmarked	?	?	?	?	?	n.d.	n.d.	n.d.	?
After 2 tides Sight records	Cross	127		2	0	0	0	0	0	129
	Line	4		5	8	1	2	0	0	20
	Unmarked	2		3	1	9	7	17	24	63
After 4 tides Collection	Cross	8	38	71	19	7	4	1	n.d.	148
	Line	1	0	2	4	3	3	1	n.d.	14
	Unmarked	0	2	2	5	7	13	16	n.d.	45

* These 16 snails were the only ones not yet moving.
† Combined marks.
n.d. = No data available.

prolonged and more drastic handling. The circumstances affecting the density experiment discussed above are not valid here since both the sighting records and the final collection were made during the first hours of the rising tide. These data estimate dispersal rather than absolute rates of movement, and some subjective assessments made during the density experiment are relevant. Rates of movement may be high (as much as 3–4 m. in 15 minutes). In the course of one tidal cycle, snails were observed to have left tracks equalling 7–8 m. However, tracks are rarely straight, and often elaborately looped, so that each individual snail tends to remain in the same general area. Observations such as these led to the proportions arranged, in the density experiment, for the larger (sampling) area and the inner (dispersal) area (40 m. by 40 m. enclosing 20 m. by 20 m.). The minimum width of the outer zone was thus 10 m. All marks appeared in the outer zone within two days, and by the sixth day considerable numbers of first-day marks were found just within the outer edge of the larger square. Actually at least one specimen of every mark was found just within the edge of the outer square during the final collection of day VI (VIF).

Analysis and Interpretation

The simplest possible estimate from capture-recapture data, involving a single recapture of a single previous mark, is the "maximum-likelihood" estimate given by the formula:

$$P_{xy} = \frac{N_y M_x}{R_{xy}}$$

where P_{xy} is an estimate of the population based on the recaptures on day y of individuals marked on day x, N_y is the total captured on day y, M_x is the number of individuals bearing a mark from day x which are "at risk" on day y, and R_{xy} is the number of recaptured marks as defined earlier. Both for this, and for other more complex estimates below, it is worth setting out the data in a trellis

Table III

Trellis: raw data transformed to single marks

Capture days:		I	II	III	IV	V	VI	VIF
Number of marked indiv. captured		0	3	23	58	67	47	273
Number of marks captured		0	3	24	60	73	55	339
Number marked I	142	—	3	20	16	26	11	60
Number marked II	132	—	—	4	21	15	13	64
Number marked III	145	—	—	—	23	28	17	83
Number marked IV	157	—	—	—	—	4	12	78
Number marked V	161	—	—	—	—	—	2	54
Unmarked indiv. captured		142	129	122	99	94	89	147
Total indiv. captured		142	132	145	157	161	136	420

array (as used by Dowdeswell, Fisher and Ford, 1940. 1949, but in the reorientated and typographically simpler form used by Andrewartha, 1961, and others). In the trellis (Table III), the raw data are transformed to single marks, and there is consequently a slight loss of information. In the trellis each horizontal row represents the recaptures of one day's marking on successive days, and each vertical column the recaptures of the available marks on one day. Diagonals across the central part represent the recaptures after an interval of one day, of two days and so on. The column headed VIF gives the final *total* number of snails captured on day VI and includes the regular sampling (column VI). On the diagonal of recaptures after a lapsed time of one day appear the recapture figures (R_{12}, R_{23}, R_{45} and Regular R_{56}) which are rejected on behavioral grounds. All the other R_{xy} data are available for calculation by this simple maximum-likelihood formula, and there are thus 16 possible estimates of P_{xy}. The estimates of P_{16}, P_{26}, P_{36} etc. derived from the VIF totals are to be preferred (since based on larger samples) to the regular VIth day series. This leaves the 12 values of P_{xy} which are calculated and form the seventh column of Table IV. These population estimates range from 733.7 (P_{36}) to 1416.8 (P_{25}), with a mean of 1,018.4, and a standard deviation (s.d.)

of 222.4. It should be noted that this s.d. is a measure of the variance of this group of 12 results, not a measure of variance of the population estimates as such. Bailey (1951, 1952) has examined the precision of such estimates of P_{xy} and shows a measure of the variance to be:

$$\text{Var. } P_{xy} = \frac{(M_x)^2 N_y (N_y - R_{xy})}{(R_{xy})^3}$$

expressed in the terms used in the present paper. Values can be calculated for the data in Table IV: for example, for the estimates over two days (P_{24}) and over five days (P_{16}) the variance values are 40,172.5 and 14,114.8, respectively. The root values, which can be considered as "standard errors" of the estimates, are 200.4 (for P_{24}) and 118.8 (P_{16}).

TABLE IV

Maximum likelihood estimate of population, simple computation

Estimate	On mark	Capture day	N_y	M_x	R_{xy}	$\frac{N_y M_x}{R_{xy}}$
P_{13}	I	III	145	142	20	1029.5
P_{14}	I	IV	157	142	16	1393.4
P_{24}	II	IV	157	132	21	986.9
P_{34}	III	IV	157	145	23	989.8
P_{15}	I	V	161	142	26	879.3
P_{25}	II	V	161	132	15	1416.8
P_{35}	III	V	161	145	28	833.8
P_{16}	I	VIF*	420	142	60	994.0
P_{26}	II	VIF*	420	132	64	866.3
P_{36}	III	VIF*	420	145	83	733.7
P_{46}	IV	VIF*	420	157	78	845.4
P_{56}	V	VIF*	420	161	54	1252.2
					Mean	1018.4

* Final totals for VIth day used here.

It is noted above that transforming the data to single marks results in a loss of information on the occurrence of multiple recaptures or double marks, which could yield an estimate of population size. The simple formula for a maximum-likelihood estimate can be adapted for double marks:

$$P_{(wx)y} = \frac{N_y\, M_{(wx)}}{R_{(wx)y}},$$

where $P_{(wx)y}$ is an estimate of the population based on the recaptures on day y of individuals with marks for both days w and x, and the other terms correspond. The numbers of double marks "at risk" on any day subsequent to the second marking can be derived from Table I, and are the terms for $M_{(wx)}$. The following values are available: $M_{(12)} = 3$, $M_{(13)} = 20$, $M_{(23)} = 4$, $M_{(14)} = 16$, $M_{(24)} = 21$, $M_{(34)} = 23$, $M_{(15)} = 26$, $M_{(25)} = 15$, $M_{(35)} = 28$, and $M_{(45)} = 4$. Rejecting the values for $R_{(12)3}$, $R_{(14)5}$ and $R_{(35)6}$ on the usual behavioral grounds, and omitting all calculations based on $R_{(wx)y} = 1$, then we have the 11 estimates of $P_{(wx)y}$ calculated and given in Table V. These range from 560 to 2100, with a mean of 1091.2, and an s.d. of 484.1. Most individual variances of these estimates would be very large because of the low double recapture rates (low values of $R_{(wx)y}$), and they are not calculated here. The fact that these estimates of $P_{(wx)y}$ based on double marks are closely comparable to the values of P_{xy} calculated earlier is a further confirmation of a lack of "capture-prone" bias in individual snails.

A modification of the simple proportional formula was proposed by Bailey (1951, 1952) to reduce positive bias. He demonstrates (Bailey, 1951) that this modified estimate has an average relative bias that is more than order of magnitude lower

Table V

Maximum likelihood estimates of population, based only on "double"-marked individuals

Capture day	On mark	N_y	$M_{(wx)}$	$R_{(wx)}$	$\frac{N_y M_{(wx)}}{R_{(wx)}}$
V	I + III	161	20	4	805.0
VI	I + III	136	20	3	906.7
VI	III + IV	136	23	2	1564.0
VIF	I + III	420	20	13	646.2
VIF	II + III	420	4	3	560.0
VIF	I + IV	420	16	5	1344.0
VIF	II + IV	420	21	11	801.8
VIF	III + IV	420	23	16	603.8
VIF	I + V	420	26	8	1365.0
VIF	II + V	420	15	3	2100.0
VIF	III + V	420	28	9	1306.7

Mean = 1091.2

at certain levels of sample and population size and, expressed in our terms, has the form:

$$P_{xy} = \frac{M_x (N_y + 1)}{(R_{xy} + 1)}$$

Bailey (1951) also proposed a satisfactory approximation for the variance of this estimate of P_{xy}. The present data are unlikely to require such correction for positive bias. However, using the above formula on the data for single marks in Table III, yields estimates (not set out in the tables) with a mean of 986.6, an s.d. of 202.9, and 'standard errors" (using Bailey's approximation) of the order of 183.4 and 115.1.

A great deal of previous capture-recapture work, particularly with fish stocks, has utilized methods involving series of census carried out on stocks in which the marks were not distinguished as to date of origin. One of the best of such methods is that originated by Schumacher and Eschmeyer (1943) involving census weighted for sample size. The Schumacher-Eschmeyer method is discussed by DeLury (1958) and Turner (1960), and theoretical arguments given by DeLury, and practical reasons by Turner, for preferring it to a maximum-likelihood method, in certain cases. In general terms, it appears that a maximum-likelihood estimate is still most efficient if sampling is truly random, and if random dispersal of marks is complete by the time of re-sampling, but that if sampling is biased for any reason a method involving weighting for sample size is to be preferred. The data on *Polinices duplicatus* can be used in a Schumacher-Eschmeyer computation. The general formula used is:

$$P(\text{Schumacher-Eschmeyer estimate}) = \frac{\sum N_d M_d^2}{\sum R_d M_d}$$

when M_d is the total number of marked *individuals* at risk on day d, N_d is the number captured on day d, R_d is the number of recaptured marked *individuals* in N_d. We are concerned here with numbers of individuals recaptured rather than number of marks, and it is necessary to use for M_d the cumulative totals for each day of all the marked individuals at risk. These can be derived from the sums of previously unmarked snails collected for marking (listed in column 2 of Table I). Thus we have as values for M_d on day II—142, III—271, IV—393, V—492 and VI—586. These values are used along with those for N_d and R_d in Table VI.

TABLE VI

Serial census method for Schumacher-Eschmeyer estimate of population

Day	M_d	N_d	R_d	(R_dM_d)	$(N_dM_d^2)$
dII	142	132	3	426	2,661,648
dIII	271	145	23	6,233	10,648,945
dIV	393	157	58	22,794	24,248,493
dV	492	161	67	32,964	38,972,304
dVIF*	586	420	273	159,978	144,226,320
				$\sum R_dM_d$ =222,395	$\sum N_dM_d^2$ =220,757,710

$\therefore \hat{P} = 992.6$

* Final totals for VIth day only used here.

The estimate of P derived by this method is 992.6. In spite of the fact that considerable information is lost by treating all marks as one type of mark, this Schumacher-Eschmeyer estimate is remarkably close to the mean of the maximum-likelihood estimates produced by Bailey's modified formula.

It is probable that the most complete utilization of capture-recapture data of the present sort is provided by a series of computations such as were developed by C. H. N. Jackson in his work on tsetse-fly populations in association with R. A. Fisher (Jackson, 1933, 1937, 1939, 1948; see also Fisher and Ford, 1947; Dowdeswell, Fisher and Ford, 1940, 1949). The theoretical bases of these methods are discussed by Bailey (1951) and by Leslie (1952), and simplified examples of the computations set out by Dowdeswell, Fisher and Ford (1940) and by Andrewartha (1961). The present data on *Polinices duplicatus* can be used both in Jackson's *positive* method, involving recapture on a number of occasions after one marking. and in Jackson's *negative* method, involving a single recapture of marks made on a series of occasions. Table VII is a trellis array of the values of R_{xy} to be used,

TABLE VII

Trellis: selected recapture data as used in Jackson computations, with calculated relative frequencies

Capture days:			III	IV	V	VIF (total)
Number marked	I	142	20 (9.7)	16 (7.2)	26 (11.4)	60 (10.1)
	II	132		21 (10.1)	15 (7.1)	64 (11.5)
	III	145		23 (10.1)	28 (12.0)	83 (13.6)
	IV	157				78 (11.8)
	V	161				54 (8.0)
Total individuals captured:			145	157	161	420

Note: the numbers in brackets are relative recapture frequencies (f_{xy}), as defined in the text.

omitting the usual ones on behavioral grounds, and using only the total captures for day VI (VIF). These values of R_{xy} are first converted to relative recapture frequencies (f_{xy}) which correspond to what the recaptures would have been if 100 had been marked and 100 captured on each successive date. These are derived by:

$$f_{xy} = R_{xy} \times \frac{100}{M_x} \times \frac{100}{N_y}$$

We have twelve available values (for f_{13}, f_{14}, f_{24}, f_{34}, f_{15}, f_{25}, f_{35}, f_{16}, f_{26}, f_{36}, f_{46} and f_{56}) and these appear in brackets below the corresponding recapture figures (R_{xy}) in the trellis of Table VII. Each vertical column with three or more values of f_{xy} gives the number recaptured on one day for an estimate by Jackson's negative method; each horizontal row with three or more values of f_{xy} represents the subsequent recaptures of one set of marks and provides one estimate by Jackson's positive method. Thus we have six possible estimates, three by each method. We have first to calculate values of z and z*, which are weighted ratios of relative recaptures (z for each positive, and z* for each negative computation). Examples of these weighted ratios are:

$$z = \frac{f_{14} + f_{15} + f_{16}}{f_{13} + f_{14} + f_{15}} \quad \text{(positive method), and}$$

$$z^* = \frac{f_{46} + f_{36} + f_{26} + f_{16}}{f_{56} + f_{46} + f_{36} + f_{26}} \quad \text{(negative method)}$$

These are then employed in calculating a reciprocal value for the population estimate, which then requires multiplication by 100×100 to convert relative frequencies back to absolute numbers. Examples of the formulae are:

$$10^4(P)^{-1} = \frac{f_{13} + f_{14} + f_{15}}{z} - (f_{13} + f_{14}) \quad \text{(positive method), and}$$

$$10^4(P)^{-1} = \frac{f_{56} + f_{46} + f_{36} + f_{26}}{z^*} - (f_{56} + f_{46} + f_{36}) \quad \text{(negative method).}$$

From the data of Table VII we have positive estimates of P of 908.3, 1720.9, and 1113.0, and negative estimates of 740.9, 1296.8, and 1054.4. The great value of the Jackson methods lies in their ability to deal with changing population densities, and these estimates above are extrapolations forwards or backwards and actually represent the population estimate on a specific day. The population of *Polinices* studied is thought to have been relatively stable over the short period of this experiment. Another advantage of the Jackson computations is that they are thus applicable in conditions where a longer delay is necessary after each release to allow marked animals to disperse and settle down. Obviously they will prove valuable with certain types of littoral populations but, in the present case, yield estimates no more valuable than the simpler ones, in spite of the more complete utilization of the data. Bailey (1951, 1952) has given methods for an approximate estimate of var. P for both positive and negative methods, but these are not computed for the present data. Leslie (1952; see also Leslie and Chitty, 1951; Leslie, Chitty and Chitty, 1953) has suggested slight elaborations of the Jackson methods, less general in application, but which can be more precise as a result of utilizing a still greater proportion of the information yielded by the data.

The above may serve to indicate which computational methods can be best applied to any future capture-recapture work on other marine benthic populations. Apart from behavioral considerations, the sample size, and the relative time-scales of sampling and of population life-cycle should be decisive. Turning to the results of the work on *Polinices duplicatus,* it seems clear that the true population level for the 1600 square meters at the time of the experiment lay close to the average values from maximum-likelihood estimates of 1018.4 (simple calculation), and of 986.6 (Bailey's modification), and from the Schumacher-Eschmeyer computation of 992.6. For comparative purposes, we can say that a close estimate is about 1,000 and, from the different variance values computed, that it was unlikely to lie outside 850–1150. Thus the density is probably about 6250 (between 5313 and 7188) per hectare, or about 2530 (between 2150 and 2900) per acre of intertidal flats.

The total area of Barnstable Harbor is approximately 3763 hectares, or 9298 acres. Of these 55% are occupied by salt marsh. The remainder consists of extensive sand flats (26%) dissected by permanent subtidal channels (19%). Throughout the sand flats (approximately 1672 hectares or 4132 acres) and channels (approximately 711 hectares or 1756 acres) there are populations of *Polinices duplicatus.* The population densities vary greatly within this area. For example, within the permanent channels densities are relatively low, while along the margins of these channels, on areas of higher organic content, the greatest densities for the harbor may be reached. On the sand flats the greatest densities are found around the level chosen for the density square in the current study. Above and below this level the population densities are usually lower.

In the central areas of the harbor particularly, it is probable that the population densities of all moon-snails have been reduced since the time of this study (summer, 1962) by a human agency. Shellfish interests have supported extensive destruction of moon-snails and *Limulus* in subsequent summers. The effectiveness of this program has not been tested and is questionable.

One additional result should be mentioned here. At the conclusion of the VIth day's collections all 420 marked and unmarked specimens of *Polinices duplicatus* were taken to the laboratory where the maximum shell diameter was measured with a dial-caliper. The total number of marked individuals recaptured at that time was 273, and their size range was 18.8 to 53.9 mm. (mean = 29.27 mm., s.d. 7.012 mm.). Individuals with double and triple marks totalled 63, with a size range 19.5 to 45.6 mm. (mean = 28.98 mm., s.d. 5.710 mm.). Total unmarked captures (VIF) was 147, with a size range 17.6 to 52.2 mm. (mean 27.95 mm., s.d. 6.853 mm.). Thus there is little evidence of any size bias as regards chance of multiple recapture. In addition, the mean values lie within the range for other population samples from elsewhere in Barnstable Harbor (Hunter, unpublished). Further, it is worth noting that the "undersized" specimens of *P. duplicatus* which were "rejected" before marking had a mean size of 12.2 mm., and made up less than 10% of each sample collected and marked (that is, less than 1.5% of the estimated population). It is thus unlikely that their removal had any significant effect on the remaining adult population.

Finally, it should be pointed out that if this work is judged to be a relatively successful demonstration of capture-recapture methods applied to a marine benthic population, this results from two features. First, only two persons were involved in the field work, both of whom had considerable experience of the general biology of *Polinices,* including its behavior patterns. Secondly, because of this experience and preliminary survey work, it was possible to set up the density experiment with the optimum time interval, sample size, and recapture rate. It is clear that the application of these methods to a benthic population of totally unknown biology could show intolerable bias.

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Summary

1. Capture-recapture methods were used to assess population density and dispersal in *Polinices duplicatus*.

2. Preliminary surveys indicated an area of 1600 sq. m. as optimal for density estimations. This yielded capture rates averaging 147 per day and the number of each mark recaptured usually made up 7.7% to 19.3% of each sample.

3. Various computational methods are applied to the data, and their values discussed. These include simple and modified maximum-likelihood estimates (with measures of their variance), a serial census method weighted for sample size, and the classical Jackson-Fisher extrapolations of relative recapture frequencies, both "positive" and "negative."

4. The two maximum-likelihood methods yield average population estimates of 1018.4 and 1091.2, and the sample-weighted census method yields a value of 992.6. With capture rates and mark frequencies as in this study on *Polinices,* these relatively simple calculations are judged adequate.

5. These estimates are equivalent to a population density for *Polinices duplicatus* of 6250 (5313–7188) per hectare, or 2530 (2150–2900) per acre.

6. Recommendations are made regarding the value of different computational methods, if capture-recapture methods are applied to other marine benthic populations. Approximate population density, sample size, and the relation of sampling-rate to population dynamics should be used to determine the appropriate procedure.

LITERATURE CITED

Andrewartha, H. G., 1961. Introduction to the Study of Animal Populations. Methuen and Co. Ltd., London, 281 pp.

Ayre, G. L., 1962. Problems in using the Lincoln Index for estimating the size of ant colonies (Hymenoptera: Formicidae). *J. N. Y. Entomol. Soc.,* **70**: 159–166.

Bailey, N. T. J., 1951. On estimating the size of mobile populations from recapture data. *Biometrika,* **38**: 293–306.

Bailey, N. T. J., 1952. Improvements in the interpretation of recapture data. *J. Anim. Ecol.,* **21**: 120–127.

DeLury, D. B., 1958. The estimation of population size by a marking and recapture procedure. *J. Fish. Res. Bd. Canada,* **15**: 19–25.

Dowdeswell, W. H., R. A. Fisher and E. B. Ford, 1940. The quantitative study of populations in the Lepidoptera, 1. *Polyommatus icarus* Rott. *Ann. Eugenics, London,* **10**: 123–136.

Dowdeswell, W. H., R. A. Fisher and E. B. Ford, 1949. The quantitative study of populations in the Lepidoptera, 2. *Maniola jurtina* L. *Heredity,* **3**: 67–84.

Evans, F. C., 1949. A population study of house mice (*Mus musculus*) following a period of local abundance. *J. Mammal.,* **30**: 351–363.

Fisher, R. A., and E. B. Ford, 1947. The spread of a gene in natural conditions in a colony of the moth *Panaxia dominula* L. *Heredity,* **1**: 143–174.

Hunter, W. Russell, and M. L. Apley, 1965. A condition of temporary hyperthermia in a marine littoral snail. *Biol. Bull.,* **129**: 408–409.

Jackson, C. H. N., 1933. On the true density of tsetse flies. *J. Anim. Ecol.,* **2**: 204–209.

Jackson, C. H. N., 1937. Some new methods in the study of *Glossina morsitans.* *Proc. Zool. Soc. London,* **1936**: 811–896.

Jackson, C. H. N., 1939. The analysis of an animal population. *J. Anim. Ecol.,* **8**: 238–246.

Jackson, C. H. N., 1948. The analysis of a tsetse-fly population. III. *Ann. Eugenics, London,* **14**: 91–108.

Leslie, P. H., 1952. The estimation of population parameters from data obtained by means of the capture-recapture method, II. The estimation of total numbers. *Biometrika,* **39**: 363–388.

Leslie, P. H., and D. Chitty, 1951. The estimation of population parameters from data obtained by means of the capture-recapture method, I. The maximum likelihood equations for estimating the death-rate. *Biometrika,* **38**: 269–292.

LESLIE, P. H., D. CHITTY AND H. CHITTY, 1953. The estimation of population parameters from data obtained by means of the capture-recapture method, III. An example of the practical applications of the method. *Biometrika,* **40**: 137–169.

LINCOLN, F. C., 1930. Calculating waterfowl abundance on the basis of banding returns. *U. S. Dept. Agric. Circ.,* **118**: 1–4.

SCHUMACHER, F. X., AND R. W. ESCHMEYER, 1943. The estimate of fish population in lakes or ponds. *J. Tennessee Acad. Sci.,* **18**: 228–249.

TURNER, F. B., 1960. Size and dispersion of a Louisiana population of the cricket frog, *Acris gryllus. Ecology,* **41**: 258–268.